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Non-linearity of Baroreceptor Nerves

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Abstract:

Denne tekst er blevet til på baggrund af et foredrag givet ved symposiet "Mathematical Models in Physiology, the Cardiovascular System and its Regulation" der blev afholdt som en del af ECMI96 konferencen. Det er tanken at nærværende tekst skal danne baggrund for en egentlig publicerbar artikel.

Det ikke lineære respons i nerveaktivitet ved et tryk-input i Carotid Sinus Arterien modelleres vha ikke-lineære rate-sensitive ordinære differentialligninger. En lang række eksperimentelt målte effekter simuleres diskuteres.

Non-Linearity of Baroreceptor Nerves

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Abstract

Two simple affector models are develop, the primitive affector model, consisting of a non-linear differential equation, and the extended affector model, consisting of three coupled non-linear differential equations. The models are both rate sensitive and linear in the (derivative of the) carotid pressure. However, the history of the time derivative of the carotid pressure enters, whereby the relative level of the carotid sinus arterial pressure is sensed. Step responses to step pressures follows from this rate sensitivity. Adaptation and asymetric response is a consequence of the historical memory. The non-linearity gives the typical sigmoidal response curves.

1 Introduction

There have been a lot of effort on modelling the baroreflex-feedback mechanism regulating the cardiovascular system. All of these focus mostly on the effector part of the feedback and less - if any - on the affector part, where the input to the feedback mechanism takes place. However, the baroreceptor function is important because baroreceptors are the first stage in the neural system regulating blood pressure and the effect of other control mechanisms, such as renal, humonal, and tissue autoregulation, is much slower. In this paper focus is made exclusively on the affector part. It follows that this part might be very important for the dynamics of the cardiovascular system when it is not in steady state [13]. More precisely the phrase "the affector part" denote the part of carotid sinus where the baroreceptor nerves are located together with the baroreceptor nerves, including the axons. In figure 1 the entire baroreflex-feedback mechanism is drawn. When a change in carotid sinus arterial pressure appears the cross-section area of these arteries change, whereby the viscoelastic wall is deformated (pressure-mechanical deformation.) The receptors at the nerve endings are located in the lateral wall of carotid sinus. The mechano-electrical transduction is taking place in these receptors themselves by an unknown coulpling mechanism [3]. Hence a change in pressure cause a deformation in the spatial

structure, which results in a change in the nerve activity of the baroreceptor nerves. This nerve activity is shortly denoted the firing rate. In section 2 of this paper a simple and an extended model, describing the highly non-linear response in firing rate to change in carotid sinus arterial pressure, are develop. In section 3 the models are analysed and compared to experimental facts. At the end a discussion, summary and outlook is presented. But first a historical surwey is given.

The first documented measurements of the baroreceptors response to change in carotid sinus arterial pressure, or shortly carotid pressure, was delivered by Bronk and Stella and reported in 1932 and 1935 [1] and [2], respectively. Since then several experiments have been made, see Thaher et al. for a more detailed discussion [19]. It shall be emphazised that when measurements are performed it is, for practical reasons, always the axonal firing rate which is measured.

The experimental conclusion is that the firing rate of the baroreceptor nerves shows several non-linear characteristics:. Firing rate increase with carotid pressure. The response exhibits treshold and saturation. Sufficient fast decrease in pressure cause firing rate to decrease below the treshold. Step change in pressure cause step change in firing rate followed by a resetting phenomena, i.e. a decay or discharge in firing rate, toward the treshold value. This resetting is called adaptation and should not be confused with a distributed time delay phenomena. The response curve is sigmoidal and shows an asymmetric behavior, like in hysteresis. However, this phenomena is not a phycical hysteresis. Finally observations indicate that the response curve for hypotensive sinus and hypertensive sinus simply is translations of the response curve for normotensive sinus to the left and right, respectively.

There have been some effort to model these non-linear characteristics of the baroreceptors. Landgren in 1952 [12] and Robinson and Sleight in 1980 [15] suggested simple functional descriptions of the response to step pressure only. Warner in 1958 [20], and in modified form in 1965 [21], Sher and Young in 1963 [16], Pointras et al. in 1966 [14], Spickler and Kezdi in 1967 [17], Franz in 1969 [8], and Srinivasan and Nudelman in 1972 [18] suggested various models based on ordinary differential equations.

These models were able to explain some, and a few even all, of the non-linear characteristics of the baroreceptors. However, the models described by differential equations make exclusively use of set-points, which are not physiologically based. Moreover, all of them incoporate each of the non-linearities separately, implying that they arise independently. In 1982 Cecchini et al. [5] demonstrated that this is not the case and Taher et al. [19] suggested in 1988 a unified model capable to establish all the non-linear characteristics of the baroreceptors. This model describe the step change in response to a step change in pressure. A continuous change in pressure was then regarded as a cascade of very small step changes, giving rise to a major bookkeeping. The excellent discussion given in this paper has served as an inspiration for the work presented here, where new comprehensive models are develop, justified and analysed. This new models are mathematically expressed in terms of non-linear ordinary differential equations.

Thereby they becomes object for mathematical analysis and easy to incoporate in models of the entire feedback mechanism [13].

2 The Affector Models

In this section a simple model together with an extended model of the response in firing rate to a change in carotid pressure are suggested. Hereby various non-linear effects are explained.

A first approach to a simple affector model is mathematically given by

$$\dot{n} = k\dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2} - \frac{1}{\tau}(n-N) \tag{1}$$

where $\dot{n}$ denotes the time derivative of the firing rate n, $\dot{P}_c$ the time derivative of the carotid pressure P_c, k a proportional constant, M the maximal firing rate, τ a characteristic time constant describing the resetting, and N the treshold, i.e. the stable equilibria of the firing rate when no change in pressure appears.

If we neglect the second term on the right hand side of equation (1) for a while, it follows that the instantaneous change in firing rate is proportional to the change in carotid pressure. This rate-sensitivity gives step responses to step inputs. However this "proportionallity" depends on the instantaneous firing rate. The change in firing rate is most sensitive to change in carotid pressure when the value of the firing rate is in the middle of it physiological range and almost insensitive near the boundary. Hereby the sigmoidal form of the response curve appears. The physiological range for the firing rate is $[0, M]$, where $M = 120$ Hz is a typical value for humans. The denominator $(\frac{M}{2})^2$ is just a normalization factor and may be adopted into the proportional constant k. It shall be emphasized that the way the firing rate enters in equation (1) is not canonical. In this case quantification is made by assuming the mathematically most simple dependents agreeing with the qualitative knowledge. Alternatively one may choose $(n(M-n)/(\frac{M}{2})^2)^{1/q}$ for a suitable choice of the constant $q > 2$. In the general case one should work with an arbitrary function fulfilling the qualitative demands. When the carotid pressure is held constant the interpretation of the second term becomes simple, it gives an exponential resetting toward the treshold value N with characteristic time constant τ. Typical value for N is $N = 35$ Hz. When a constant increasing carotid pressure $\dot{P}_c = \tilde{k}$ is applied the saturation level is given by

$$n_+ = \frac{M}{2}\left(1 - \frac{M}{4k\tilde{k}\tau} + \sqrt{(\frac{M}{4k\tilde{k}\tau} - 1)^2 + \frac{N}{k\tilde{k}\tau}}\right)$$

Notice, that $n_+ \to M$, for $\tilde{k} \to \infty$. Similar when a constant decreasing carotid pressure $\dot{P}_c = -\tilde{k}$ is applied then the firing rate tends to

$$n_- = \frac{M}{2}\left(1 + \frac{M}{4k\tilde{k}\tau} - \sqrt{(\frac{M}{4k\tilde{k}\tau} + 1)^2 - \frac{N}{k\tilde{k}\tau}}\right)$$

and $n_- \to 0$, for $\tilde{k} \to \infty$.

When n is smaller than $\frac{M}{2}$, $\dot{n}$ is more sensitive to a continuous increasing carotid pressure than to a continuous decreasing carotid pressure, because of the non-linearity described by equation (1). For n larger than $\frac{M}{2}$ the situation is reversed. Several authors have noticed that the firing rate is not equally sensitive to raise and lowering in carotid pressure, see for example [11] and [21]. However, this asymmetry in sensitivity is not due to separate effects with different weights of positive and negative change in carotid pressure, as some authors claim, but rather to the non-linearity, as mentioned.

Before discussing the model further, two alternative but mathematical equivalent formulations are given. First equation (1) is rewritten in integral form as

$$n = N + \int_{-\infty}^{t} e^{-(\frac{t-s}{\tau})} [k\dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2}] \, ds \tag{2}$$

where t denotes the time and s the dummy variable of integration. We notice that equation (2) is mathematically equivalent to formula known from some systems with distributed time delay. However, in our case there is no physical time delay. In fact, the resetting phenomena is very complex and is partly due to chemical diffusion in the nerve cells. Anyway, this analogy suggest that the exponential kernel in equation (2) might be substituted by another kernel. We return to this generalization below. The second way of rewritting equation (1) is by introducing the deviation, $\Delta n = n - N$, in n from its treshold value N. Then equation (1) reads

$$\Delta\dot{n} = k\dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2} - \frac{1}{\tau}\Delta n \tag{3}$$

Experimental data, see figure 2, indicate that the resetting is not given by just one exponential, as suggested. Therefor the exponential kernel in equation (2) is substituted by a sum of three exponentials

$$n = N + \int_{-\infty}^{t} (k_1 e^{-(\frac{t-s}{\tau_1})} + k_2 e^{-(\frac{t-s}{\tau_2})} + k_3 e^{-(\frac{t-s}{\tau_3})}) [\dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2}] \, ds \tag{4}$$

where τ_1, τ_2 and τ_3 are three characteristic time constants, characterizing different baroreceptor types. (Receptors are usually divided into different types, A, B and C fibres, due to their trasmission speed. The fast A fibres are further divided into α, β, and γ receptors). k_1, k_2, and k_3 denote the weighting of the contribution from each receptor type. The number of exponentials used is not canonical but reflects the lowest possible numbers to get sufficient agreement with the experimental data, compare figure 2 and 3. On the other hand the number should not be greater than the number of known receptor types, which is 6. In the literature measured values of the τ's, the k's and M is reported for some animals [2], [7], [9], [8], [12] and [15]. In this paper the norminal values $\tau_1 = 0.5$, $\tau_2 = 5.0$, $\tau_3 = 500$ seconds, $k_1 = 1.0$, $k_2 = 0.5$, $k_3 = 1.0$ Hz/mmHg, and $M = 120$ Hz is usually used, unless otherwise stated.

The physiological significance for having several characteristic time constants, as in equation (4), is that the term with the smallest time constant τ_1 (≈ 0.5 seconds) is primarily sensitive to momentary changes in carotid pressure, $\dot{P}_c(t)$, whereas the term with the largest time constant τ_3 (≈ 500 seconds) behave like a weighted average in the sense that it is not only dependent on the momentary value of $\dot{P}_c(t)$ but on the "integrated" value as well. The term with the intermediated time constant τ_2 (≈ 5 seconds) contributed as a combination. More precisely, each term depend not only on the momentary value of $\dot{P}_c(t)$, but on its history, as well, and on the "time horizon" given by the coresponding value of the time constants. So the rate sensitive models, given by equation (3) and (5) below, depends both on $\dot{P}_c(t)$ and on P_c, in the sense just described, and not only on $\dot{P}_c(t)$.

Equation (4) can't be rewritten as one differential equation analogue to equation (1). However, introducing the deviations Δn_1, Δn_2, and Δn_3 from the treshold value N, such that $\Delta n_1 + \Delta n_2 + \Delta n_3 = n - N$, it becomes possible to rewrite equation (4) as three coupled non-linear ordinary differential equations as follows

$$\begin{aligned} \Delta\dot{n}_1 &= k_1 \dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2} - \frac{1}{\tau_1}\Delta n_1 \\ \Delta\dot{n}_2 &= k_2 \dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2} - \frac{1}{\tau_2}\Delta n_2 \\ \Delta\dot{n}_3 &= k_3 \dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2} - \frac{1}{\tau_3}\Delta n_3 \end{aligned} \tag{5}$$

Physiologically these firing rates are trasmited in separate nerve fibers, whereby the central nervous system has the possibility to use the information separately or weighted. This may be very important when different control mechanism are considered, for example is the control of the venous pool not sensitive to short time pertubations whereas the control of the heart rate usually is. Furthermore, these weighting parameters may be object for physiological control as well as sensitive to outer circumstances, such as temperature. However, for the consideration made in this paper the weighting parameters are assumed constant and only the superposition of the firing rates will be of interest.

In the following the model given by equation (5) will be denoted "the extended affector model" and the former, given by equation (1), "the primitive affector model".

3 Analysis and Validation

In this section the models are analysed and compared to experimental facts. Simulated responses are shown to agree with experimental data to a remarkable degree.

Assuming a step input in carotid pressure, $\dot{P}_c = K\,\delta(t - t_0)$, equation (4)

has the solution $n = N$, for $t < t_0$, and

$$n = N + K\,(k_1 e^{-(\frac{t-s}{\tau_1})} + k_2 e^{-(\frac{t-s}{\tau_2})} + k_3 e^{-(\frac{t-s}{\tau_3})}) [\dot{P}_c \frac{n(M-n)}{(\frac{M}{2})^2}]$$

for $t \geq t_0$. In 1980 Brown measured the response in firing rate to a step-input in carotid pressure [3]. This is shown in figure 2. The simulated result based on the extended affector model, given by equation (5), is shown in figure 3. The agreement is remarkable except for the gap which appear in data after the firing rate has dropped to zero. Physiologically this is a postexitatory depression due to the electrogenic Na^+ pump [3].

The response in firing rate to a continuous changing carotid pressure pulse profile was first measured by Bronk and Stella, as mentioned. In 1967 Christensen, Warner and Pryor replicated the experiment [6]. Figure 4 shows the simulated response to a typical puls pressure profile in humans. The figure also shows that the response Δn_1, it is very sensitive to steep changes and the response Δn_3, which behave more like the input. The response Δn_1 shows a very fast resetting, whereas Δn_3 follows the pulse profile in form. Due to the non-linearity the total response of the extended affector model is not just a sum of the three separate responses. However, the superposition is clearly sensitive to both the level of and the change in carotid pressure. The response agree to a sufficient degree with those reported in the literature, see [6], [11]. We emphasize that it is not the same pulse profile which is used.

Coleridge et al. documented in 1981 an asymetric response of baroreceptors to increasing and decreasing pressure [5]. Figure 5 shows these measurements and the simulated asymetric response, based on the extended affector model. This asymetric response is frequently called a hysteresis loop. However, it does not represent a physical hysteresis phenomena but rather the fact that the change in carotid pressure, $\dot{P}_c$, is positive when the pressure increase and is negative when it decrease. Consider the simple affector model develop above and assume $\dot{P}_c = \pm k_0$, + when pressure increase and − when it decrease. Then equation (1) is equivalent to

$$\frac{dn}{dP_c} = k\frac{n(M-n)}{(\frac{M}{2})^2} \mp \frac{1}{k_0 \tau}(n - N) \tag{6}$$

From equation (6) it follows that the slope of the curve is greater when the pressure is increasing than when it is decreasing, for firing rate less than the treshold value, i.e. for $n < N$, and that the slope is smaller when the pressure is increasing than when it is decreasing, for firing rate larger than the treshold value, i.e. for $n > N$. In other words, the resetting interfere constructively with the pressure generated change when it is toward the treshold and destructively when pressure force it away from the treshold.

In 1981 Igler et al. reported mesurements showing that the response curve for hypotensive sinus is just a translation to the left of the normotensive curve

[10]. This is shown in figure 6 together with simulations of the response for hypotensive, normotensive and hypertensive sinuses. These phenomena are explained by a pertubation of the initial values in the model. The physiological cause to this pertubation is not well understood [10].

Figure 7 shows how the primitive affector model responds to a sinus pressure input, for two different frequencies. When the input frequency is much larger (a factor 10) than the characteristic frequency of the resetting, $\frac{1}{\tau}$, the response is oscillatory with a relatively large amplitude, i.e. of the same order as the amplitude of the oscillations of the input signal. The average firing rate is approximately 60 Hz (the response isn't sinus shaped due to the non-linearity.) When the input frequency is much smaller (a factor 10) than $\frac{1}{\tau}$, the response still oscillate, but the amplitude is then relatively small, i.e. a factor 10 smaller than the amplitude of the oscillations of the input signal. The average firing rate is again approximately 60 Hz. This reduction in response amplitude can be explain by the following approximation. Negleting the second order Δn-term in equation (3), the solution is

$$\begin{aligned} \Delta n = \quad & n_0 e^{\{c_1 \sin(\nu t)\}} e^{-\{\frac{t}{\tau}\}} \\ & + c_2 \nu \int_0^t e^{-\{\frac{t-s}{\tau}\}} \cos(\nu s) e^{\{2c_1 \cos(\frac{\nu}{2}(t+s)) \sin(\frac{\nu}{2}(t-s))\}} \, ds \end{aligned} \tag{7}$$

for a sinus input $P_c(t) = A\sin(\nu t)$, where $c_1 = \frac{kA(M-2N)}{(\frac{M}{2})^2}$, $c_2 = \frac{kAN(M-N)}{(\frac{M}{2})^2}$ and $\Delta n(0) = n_0$. The first term in equation (7) describe the transient, it vanish for $t \gg \tau$. The second term represent the response when $t \gg \tau$. In the case $M = 2N$ it follows by straight forward calculations that, after the transient,

$$\Delta n \approx k \frac{N(M-N)}{(\frac{M}{2})^2} A \nu \tau \cos(\nu t)$$

for $\nu \ll \frac{1}{\tau}$ and

$$\Delta n \approx k \frac{N(M-N)}{(\frac{M}{2})^2} A \sin(\nu t)$$

for $\frac{1}{\tau} \ll \nu$. So the amplitude is much smaller in the first case ($\nu\tau \ll 1$), i.e. for small frequencies, than in the last case ($\nu\tau \gg 1$), i.e. for large frequencies. Moreover one notice a phase shift by $\frac{\pi}{2}$ in the response for $\frac{1}{\tau} \gg \nu$, which also is observed on figure 7. The general situation is more complex, but an investigation gives the same conclusion wrt. the amplitude.

The same scenaria is represented in figure 8 for the extended affector model, given by equation (5). The effect of the input frequency on the response is qualitatively similar. However, the damping effect of the amplitude is then less pronounced. Moreover, the average response is small for low frequencies compared to those for large frequencies.

4 Discussion, Summary and Outlook

Two simple affector models are develop, the primitive affector model, consisting of a non-linear differential equation, and the extended affector model, consisting of three coupled non-linear differential equations. The models are both rate sensitive and linear in the (derivative of the) carotid pressure. However, the history of the time derivative of the carotid pressure enters, whereby the relative level of the carotid pressure is sensed. The step response to step pressure follows from this rate sensitivity. This history is described by exponential weighting factors. The adaptation phenomena is due to these weighting factors. Furthermore, the asymetry response in firing rate is also explained by these weighting factors. When a sinus input pressure is used the amplitude of the response depends on the frequency of the input pressure. For slowly varying (low frequency compare to the characteristic frequency of the adaptation phenomena) pressure the amplitude is smaller than for quickly varying (high frequency) pressure. The non-linearity appearing is in the firing rate itself. This gives the characteristic sigmoidal response curves.

The models presented here are based on experimental facts together with simplicity arguments. Hence it is ad-hoc models. But hopefully they will give some ideas to understand the underlying mechanisms. Indeed these models indicates an intrinsic coherent narrative. However, the postexitatory depression is not included in the models. This will be object for further investigations. It might be done in an ad-hoc manner, for example based on measurements reported by Brown and Brown et al. in [3] and [4], respectively.

Furthermore it is the goal for further research to investigate and understand the underlying mechanism of the mechano-electrical transduction in the receptors themselves. Also the non-linearity will be investigated with respect to theoretical understanding. It is claimed by Brown that the Mechano-electrical transduction of the receptors themselves is linear and that the non-linearity is due to the pressure-mechanical deformation of the viscoelastic wall of the carotid sinus [3]. Therefore an explanation of the non-linearity will be seek in a modelling of the mechano-electrical transduction of the viscoelastic wall of carotid sinus.

Finally an investigation of how the different nerve fibers, which are shown to be sensitive to different domains of frequencies, influence different parts of the control loop, i.e. how they contribute in steering the heart rate, the contractility of the heart, the resistance of the arteries and arterioles, the capacitance of the vessels, and the venous pool (unstress volume.)

Some research is still to be done, new questions arise from new answers to older questions. The present work indicates an intrinsic coherent narrative of the functioning of the baroreceptor nerves. The models are capable to cash the various phenomena discussed to surprisingly high degree of accuracy.

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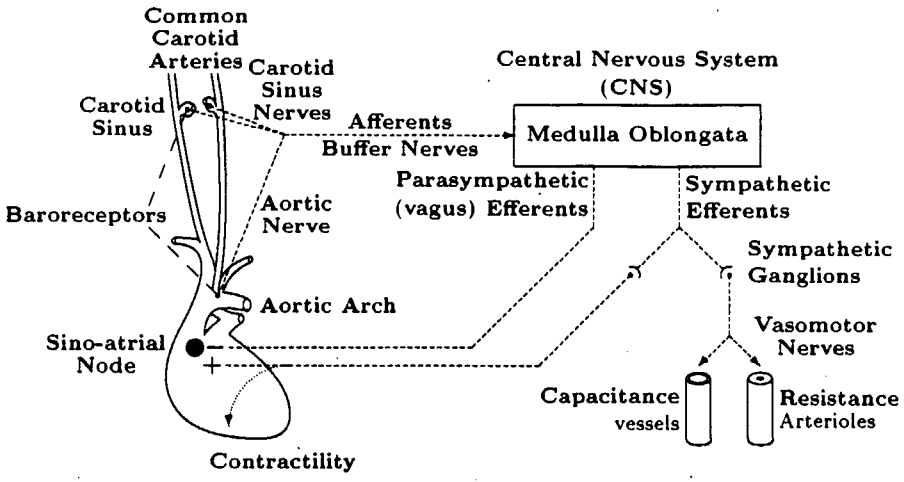

Figure 1: The entire baroreceptor feedback system. The baroreceptors are located in the lateral wall of carotid sinus. When responses are measured it is usually done in the axons of the carotid sinus nerves.

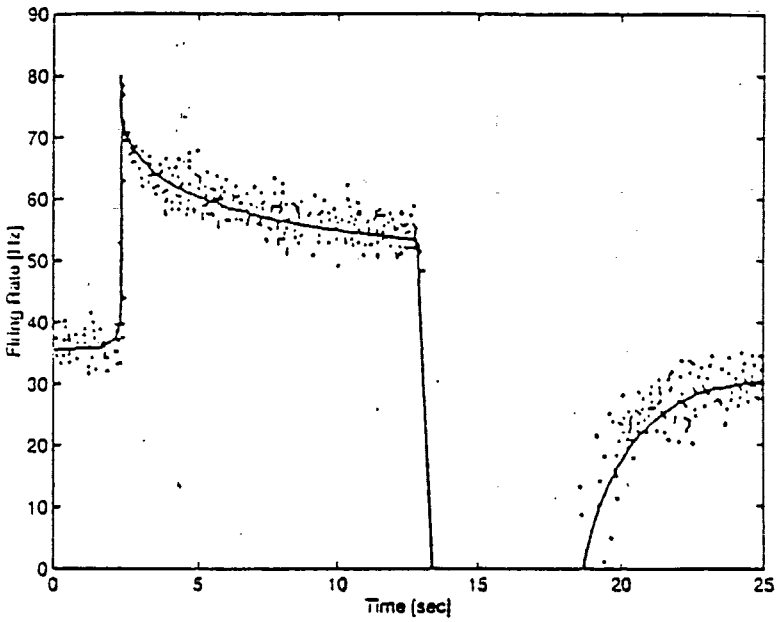

Figure 2: Response to a step input pressure as reported by Brown, [3] (printed with permission.) Pressure increase stepweise from 170 mmHg to 178 mmHg at 2.5 seconds and decrease from 178 mmHg to 170 mmHg at 12.5 seconds. Pressure is held constant else. Notice the step responses and the adaptations (resetting) toward the treshold

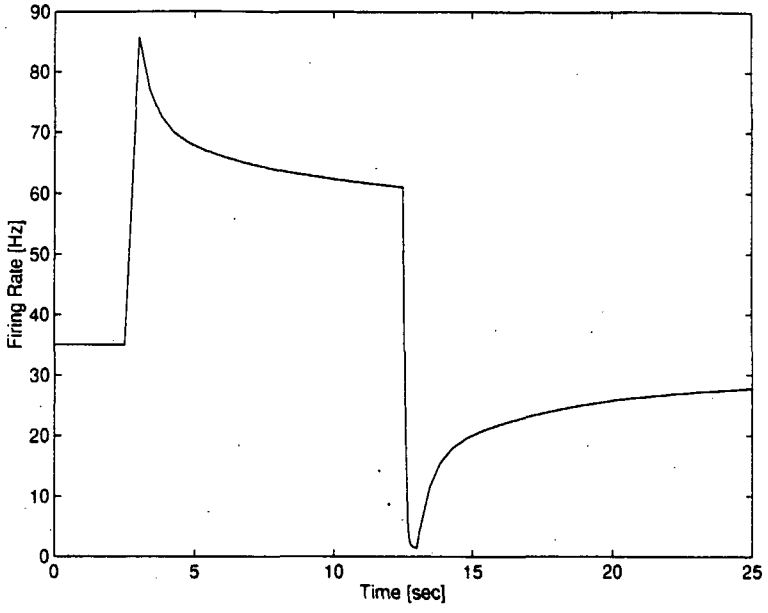

Figure 3: The response to a step input pressure based on the extended affector model. The input pressure increase from 170 mmHg to 178 mmHg at time 2.5 seconds and decrease again at time 12.5 second to the initial level. Except for the postexitatory depression gap appearing on figure 2 agree pretty well with the measurments shown.

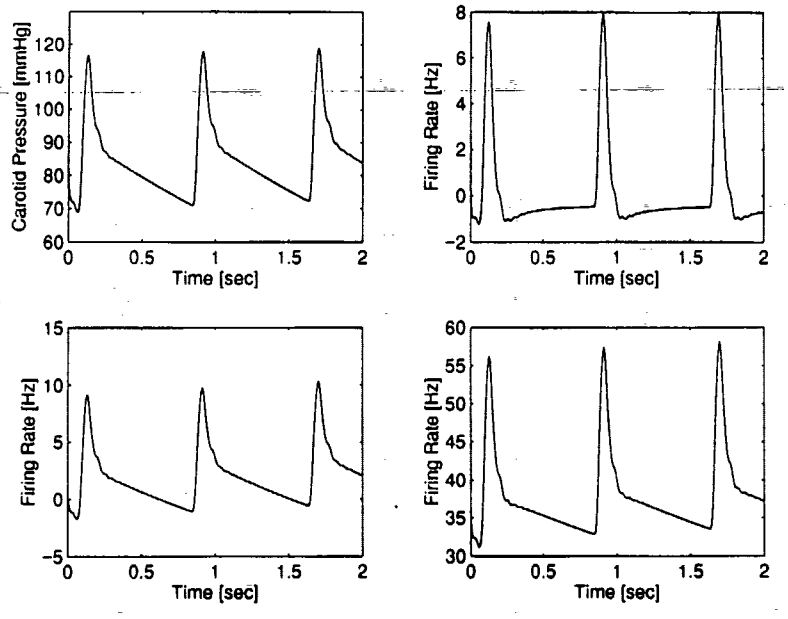

Figure 4: The response in firing rate to a typical pulse profile of humans. Upper left: The input pulse profile. Upper right: The response Δn_1 is very sensitive to steep changes ($\tau = 0.1$ seconds.) The lower left: The response Δn_3 behave like the input ($\tau = 500$ seconds.) The response Δn_2 is omitted. The lower right: The total response from the extended affector model, with the τ's =0.1, 10, and 500 seconds, respectively. Notice that the response Δn_1 shows a very fast resetting, whereas Δn_3 follows the pulse profile in form. Due to the non-linearity the total response of the extended affector model is not just a sum of the three separate responses. However, the superposition is clearly sensitive to both the level of and the change in carotid pressure. The response agree to a sufficient degree with those appearing in the literature, see for example [6], [11].

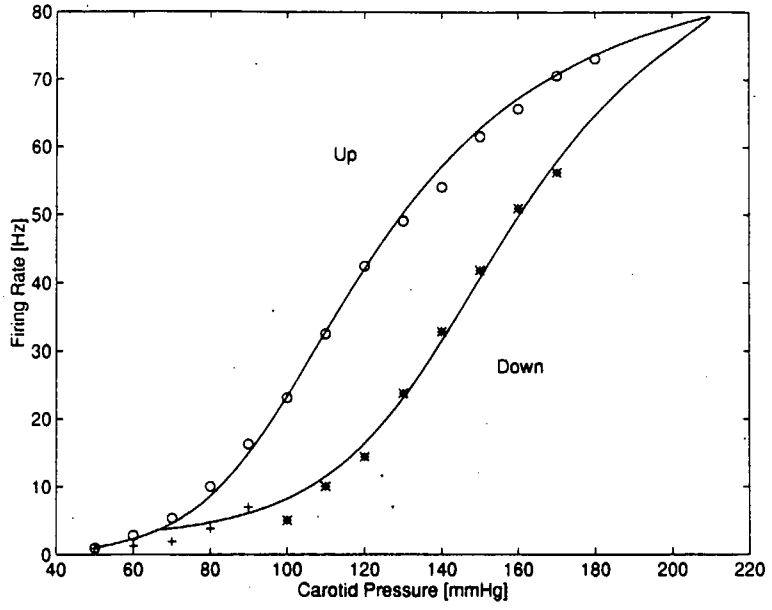

Figure 5: The asymmetric response in firing rate to increasing and decreasing carotid pressure in anesthetized dogs. Open circles indicates measurement when pressure is raised. Stars and pluses indicates different series of measurements. Stars when pressure is lowered from 170 mmHg (n = 56 Hz) to 100 mmHg (n = 5 Hz) and pluses when lowered from 100 mmHg (n = 23 Hz), indicated by an open circle, to 50 mmHg (n = 1 Hz). (Data is adopted from [5].) Solid curves indicates responses obtained by simulations, based on the extended affector model, given by equation (5), with M = 105 Hz. The curve for increasing pressure, labeled "Up", was given by $\dot{P}_c$ = 1.37 mmHg/sec and runs from 1 mmHg to 210 mmHg in 160 seconds. The curve for decreasing pressure, labeled "Down", was given by $\dot{P}_c = -1.37$ mmHg/sec and runs from 210 mmHg to 3.6 mmHg in 154 seconds. The closed curve is sometimes refered to a a hysteresis loop, however it is not a physical hysteresis phenomena.

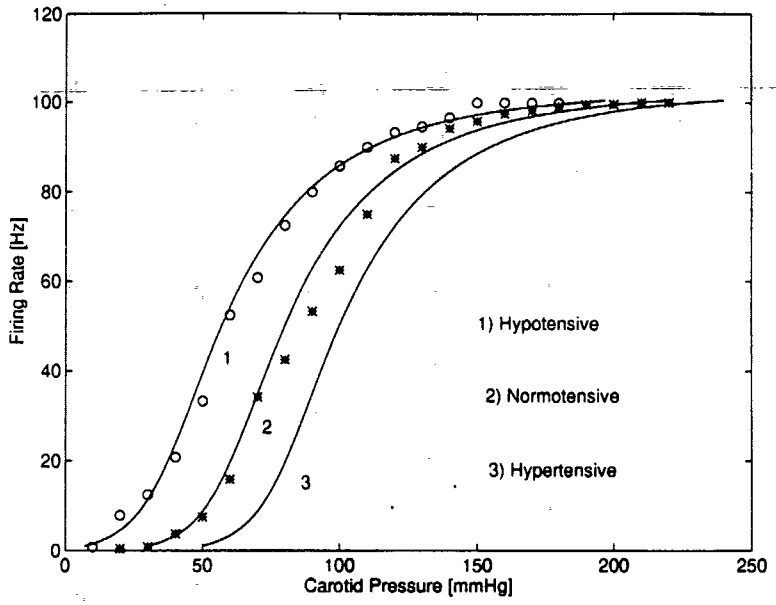

Figure 6: The response curves for normotensive, hypotensive and hypertensive sinuses in anesthetized dogs. Circles indicates measured for hypotensive sinus and stars for normotensive sinus (data is adopted from [10].) The corresponding simulated ones together with one showing hypertensive sinus are drawn by solid curves. Initial values was 0.8 Hz for 6.9, 30.6 and 50 mmHg, for 1) hypotensive, 2) normotensive, and 3) hypertensive sinuses, respectively.

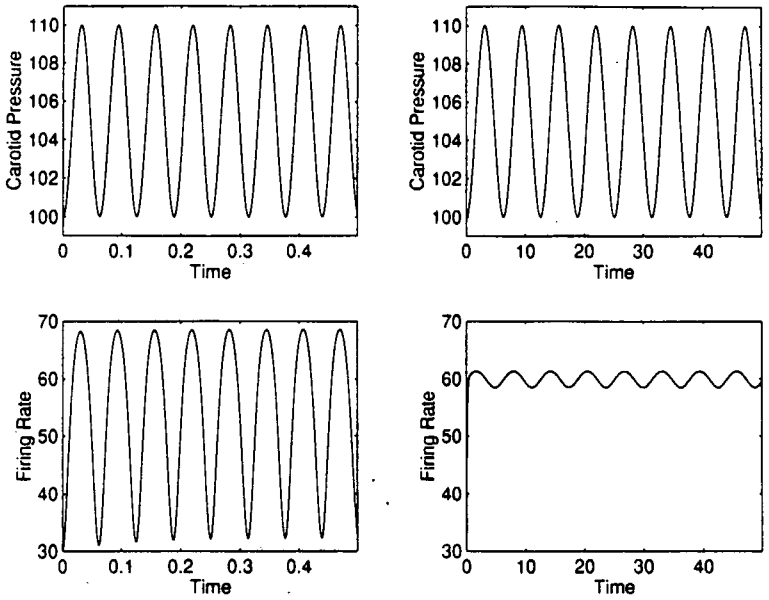

Figure 7: Responses of the primitive affector model, given by equation (1), to a sinus formed input, $A\sin(\nu t)$, for different frequencies. The first row shows the input signals in mmHg and the second row shows the corresponding resposes in Hz. The ordinate axis shows time in seconds. The left colum shows the input and the reponse for high frequency, $\nu = 100$ Hz, and with $\tau = 0.1$ second, whereas the second colum shows the input and the reponse for low frequency, $\nu = 1.0$ Hz, and with $\tau = 0.1$ second. The resonse has much smaller amplitude for low frequencies than for high frequencies. By linear approximation to equation (1) it follows that the response for small frequencies, i.e. $\nu \ll \frac{1}{\tau}$, is $\Delta n \propto \nu\tau\cos(\nu t)$, and for large frequencies, i.e. $\nu \gg \frac{1}{\tau}$, is $\Delta n \propto \sin(\nu t)$. The predicted phase shift is also observed for large frequencies.

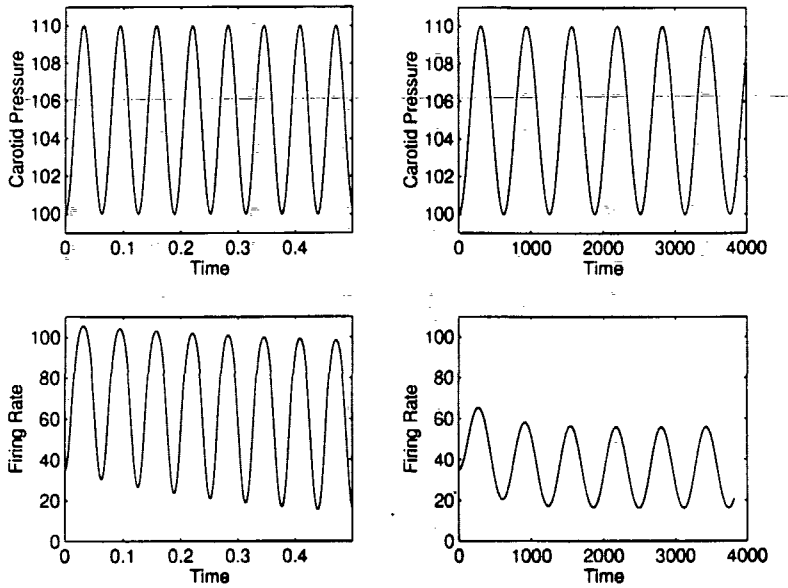

Figure 8: Responses of the extended affector model, given by equation (5), to a sinus formed input, $A\sin(\nu t)$, for different frequencies. The first row shows the input signals in mmHg and the second row shows the corresponding resposes in Hz. The ordinate axis shows time in seconds. The left colum shows the input and the response for high frequency, $\nu = 100$ Hz, and with $\tau_1 = 0.5$, $\tau_2 = 5.0$, and $\tau_3 = 500$ second, whereas the second colum shows the input and the reponse for low frequency, $\nu = 0.01$ Hz, and the same values of the τ's. As for the primitive affector model, the response has smaller amplitude for low frequencies than for high frequencies, but the effect is then less pronounced.

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Karen Birkelund, Bjørn Christensen
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Erland Brun Hansen

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Vejleder: Mogens Niss

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Om sære matematiske fisks betydning for den matematiske udvikling

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af: Linda Kyndlev, Kare Fundal, Kamma Tulinius, Ivar Zeck

Vejleder: Jesper Larsen

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Et 1.modul fysikprojekt

af: Karen Birkelund, Stine Sofia Korremann

Vejleder: Dorthe Posselt

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Projektrapport

af: Trine Andreasen, Tine Guldager Christiansen, Nina Skov Hansen og Christine Iversen

Vejledere: Gestur Olafsson og Jesper Larsen

245a+b /93 Time-Of-Flight målinger på krystallinske halvledere
Specialerapport

af: Linda Szkotak Jensen og Lise Odgaard Gade

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246/93 HVERDAGSVIDEN OG MATEMATIK - LÆREPROCESSER I SKOLEN

af: Lena Lindenskov, Statens Humanistiske Forskningsråd, RUC, IMFUFA

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by: Jeppe C. Dyre

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